

Identifying and Characterizing Dominant Plants as an Indicator of Community Condition

Christin B. Frieswyk^{1,†}, Carol A. Johnston², and Joy B. Zedler^{1,*}

¹*Department of Botany
University of Wisconsin-Madison
Madison, Wisconsin 53706*

²*Department of Biology and Microbiology, Box 2207B
South Dakota State University
Brookings, South Dakota 57007*

ABSTRACT. Dominant species play key roles in shaping community structure, but their behavior is far from uniform. We speculated that recognition of different behaviors (determined objectively) would be an indicator of the condition of plant communities. We developed a species dominance index (SDI) to identify dominant species and compare their behavior across multiple spatial scales. The SDI is based on three attributes (mean cover, mean species suppression, and tendency toward high cover), and it identifies up to 38 dominants within 74 Great Lakes coastal wetlands. Dichotomizing each of the attributes in a 2×2×2 matrix produced seven dominant behaviors, or forms, all of which occurred in Great Lakes wetlands. Species showed different dominant forms among locations and aggregation scales. Showing predominantly “monotype” form, invasive *Typha* was the taxon that was most often dominant in the samples. By quantitatively measuring dominance and describing dominance form, SDI can add insight into community change and is a useful addition to indicators of community condition.

INDEX WORDS: Dominance, Great Lakes, indicator, *Typha*, vegetation, wetlands.

INTRODUCTION

Determining the condition of a plant community is increasingly important as vegetation responds to anthropogenic stress, exotic species invasions, abiotic disturbances, and new management approaches (e.g., Godefroid and Koedam 2003, Abella and Covington 2004). Whether vegetation changes are unintentional or deliberate, land managers need indicators of community condition to use in deciding when to respond with management action, and in determining the effectiveness of their management efforts, both at local and regional scales (Ludwig *et al.* 2004; A. Vargas, Wisconsin Coastal Management Program, pers. comm.). Indicating community condition can be complicated when plant communities are naturally dynamic, like they are in Great Lakes coastal wetlands, where communities change

in response to natural variations in lake level (van der Valk 1981).

Substantial information about both abiotic and biotic properties of a plant community is conveyed simply by identifying the dominant species (as in Clements 1916, Whittaker 1965). Through their architecture, physiology, growth, and phenology, dominant plants determine overall community structure, such as biomass and canopy strata (Richards 1996) and ecosystem engineering (Malmer *et al.* 2003); soil properties (Bardgett *et al.* 1999); pathways of succession (Fastie 1995); ecosystem properties, such as nutrient cycling (Allison and Vitousek 2004) and fire regimes (Taylor 2000); micro-habitats for subordinate species (Grime 1998); and even hydrological conditions (Simberloff and Von Holle 1999). Dominant plants can exert strong influence by their abundance, height, shade, root and rhizome biomass, or chemistry (e.g., allelopathy). In sum, dominant species greatly affect both physical and biological condi-

*Corresponding author. E-mail: jbzedler@wisc.edu

†Present address: Cleveland Botanical Garden, 11030 East Boulevard, Cleveland, OH 44106, 216.707.2802, f 216.721.1694, cdejong@cbgarden.org

tions, and it makes sense to use them to examine community condition.

The behavior of a dominant species and its relationship to other species are not necessarily constant, however. A dominant species can be highly competitive in a core habitat or able to tolerate stress in a peripheral habitat (Wisheu and Keddy 1992). It can make up a majority of stems in a plot or less than the majority. Species richness can also vary with different dominants (Denslow and Hughes 2004). A particular species can vary in its dominance or dominate wherever it occurs (Lavoie *et al.* 2003). If it is variable, a species' status as a dominant could change in space and time (Hanski 1982) or under different environmental conditions (Walker *et al.* 1999). It may facilitate neighbors under one environmental condition and suppress them under another, as when cattails (*Typha* spp.) increase in abundance during eutrophication (Woo and Zedler 2002).

We speculate that dominance behavior differs both among and within species and that plant community conditions can be evaluated by comparing the species that are dominant and the form of their dominance. Furthermore, because changes in dominance behavior could occur irrespective of changes in the identity of the dominant species, the form of dominance could be a useful indicator in dynamic systems like Great Lakes coastal wetlands. Before further developing the idea of dominance behavior, we clarify terminology by reviewing the definition of "dominance," its use in the literature, and the assumptions behind the concept.

In textbooks, dominants are species that are the most abundant; a more restrictive definition requires that a dominant species control its habitat and the presence and performance of other species (Carpenter 1956, Greig-Smith 1986). Because it is hard to assess "control," it is common to assume that abundant species control their habitat and associates (Grime 1998). Dominance, then, is most often based on some measure of abundance, but the abundance at which a species becomes dominant is rarely mentioned. Few authors define their use of "dominance:" for some, it is a measurable quality that every species has (e.g., Robinson *et al.* 1995, Hector *et al.* 2002), while for others, it is a position held by some species and not others (e.g., Clark *et al.* 2001, Smith and Knapp 2003). For still others, dominance is a measurable quality of a community that is quantified using evenness indices (e.g., Potvin and Vasseur 1997, Dangles and Malmquist 2004). On occasion, dominance is used to describe

both the community and individual species, without explaining either use (e.g., Howe and Brown 1999).

A few authors characterize dominant plants in relation to the number of co-occurring species. Theodose and Bowman (1997) call those that coexist with many species, such as alpine tundra sedges, "conservative dominants." In contrast, Hodgson *et al.* (1998) described abundant plants of species-poor assemblages as "aggressive dominants." Invasive or transformer species (Richardson *et al.* 2000), such as *Phalaris arundinacea* (reed canarygrass) and *Typha x glauca* (hybrid cattail), behave in this way, tending to exclude other species and create monotypic stands (Galatowitsch *et al.* 1999). While not quantitative, these distinctions begin to address the different roles and behaviors of dominant species.

To assist managers in evaluating community condition, we sought an objective approach for identifying dominant species, and a simple means of typing their behavior based on data that are readily available or rapidly acquired. Within a large data set collected from Great Lakes coastal wetlands, we looked for three attributes of dominance that could be combined to form an index comparable to the "importance value" developed for woody vegetation (Curtis and McIntosh 1951). Then, inspired by Rabinowitz's (1981) characterization of seven forms of rarity, we used a 2×2×2 matrix to separate dominance types based on the degree of influence of each attribute. Note that we are not proposing a scheme for defining the opposite of rarity (commonness), but to derive types of dominance. The dichotomization of each of three attributes of dominance into "high" or "low" led us to identify seven potential forms of dominance, the eighth combination (all attributes "low") not being considered dominant.

Here we develop an index to identify the dominant species, explore seven forms of dominance, and consider the utility of dominance form as an indicator of community condition. With data from the Great Lakes Environmental Indicator (GLEI) project, we characterize dominance using plot data aggregated at multiple scales (wetland, lake, and regional) for dozens of species, hypothesize that species will exhibit different forms of dominance depending on location and scale, and show how the identity and form of dominant species can be used to indicate community condition.

METHODS

Data Set

We focused on plant cover data from a large data set on herbaceous coastal wetlands acquired by our vegetation subproject of the GLEI project in the summers of 2001 and 2002. Three sampling teams (see acknowledgments) collected data from 74 wetlands that represent a random sample of all U.S. Great Lakes coastal wetlands stratified to include a gradient of environmental conditions and three geomorphic types: coastal, riverine, and protected (Danz *et al.* 2005). In each wetland, transects were randomly placed perpendicular to the perceived water gradient, i.e., moving from water's edge to the upland. Plots, 1-m² in area, were then randomly placed along 20-m segments of these transects with a non-random plot at the "wet end" of the each transect. The number of plots sampled in each wetland was proportional to the size of the wetland. In each plot the species rooted within the plot were visually assigned one of six cover classes (1 = < 1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, and 6 = > 75%) modified from Braun-Blanquet (1932). Species names follow the Integrated Taxonomic Information System (www.itis.usda.gov). Visual assignment of cover classes was calibrated daily within sampling teams and yearly among sampling teams. Sampling followed a quality assurance protocol, and tests for discrepancies among sampling teams were performed (Kercher *et al.* 2003). Because cover was sampled by species in 1-m² plots, species richness per plot and frequency of occurrence across three aggregation scales—wetlands, lakes, and the entire five-lake Laurentian Great Lakes region—could also be computed from the data set.

Potentially Dominant Species

Because we designed the SDI to focus on variable attributes of a dominant species, we first evaluated every species' potential to be dominant using two criteria for dominant species. First, a dominant species must be "influential" in at least one 1-m² plot (appropriate, because species interact at this scale; Olff and Bakker 1998) within the area of interest. We assumed a positive relationship between abundance and influence (Grime 1998). After examining six potential definitions, we defined an influential species as having > 25% absolute cover and the most cover of any species in a plot. Second, we viewed frequent occurrence as a requirement of

dominance, not an attribute, since a species that strongly influences its community must occur frequently. An ecologically meaningful minimum frequency of occurrence would be the inverse of the expected number of communities. At the wetland scale, we chose a minimum frequency of occurrence of 1/3 of the plots, because three plant communities, deep marsh, shallow marsh, and wet meadow, are expected in Great Lakes coastal marshes. At the lake and region scale, the three plant communities can occur within three geomorphic wetland types, and thus a minimum frequency of 1/9 of the plots sampled was used. These criteria found 78 species to be potentially dominant in at least one wetland, 53 to be potentially dominant in at least one lake, and 12 to be potentially dominant in the region. While the influence and frequency cut-offs are both specific to the vegetation type and abundance measure in question, the principles behind them are applicable to other vegetation types and abundance measures.

The Species Dominance Index

We modeled SDI after Curtis and McIntosh's (1951) importance value and calculated it for each potentially dominant species. We used variables that measured each of three attributes of dominance: cover as a measure of abundance (traditionally used to assess dominance), species suppression (few species associated with a "dominant" species at the 1-m² scale indicating greater dominance), and tendency toward high cover (how likely a species is to be abundant when it occurs, indicating spatial structure of the "dominant" species). We derived measures for each attribute of dominance from the cover data available in the GLEI database as follows. Mean cover (MC) measures the abundance of a potentially dominant species by averaging the mid-point of recorded cover classes of that species. Values of zero were used when a species did not occur in a plot. Mean species suppression (MSS) measures the number of species associated with a potentially dominant species. It is the mean of the inverse of the number of species (1/number of species) in a plot where the potentially dominant species is influential. Tendency toward high cover (THC) is the ratio of the number of times a potentially dominant species is influential in a plot to the number of times it is present in a plot. The species dominance index, then, was computed as follows:

$$\text{SDI} = (\text{MC} + \text{MSS} + \text{THC})/3$$

TABLE 1. Theoretical framework for seven forms of dominance based on the dichotomization of three attributes.

Mean cover (MC)		High		Low	
Mean species suppression (MSS)		High	Low	High	Low
Tendency toward high cover (THC)	High	1. Monotype	3. Matrix	5. Compressed	7. Patchy
	Low	2. Ubiquitous	4. Diffuse	6. Aberrant	Not dominant

for potentially dominant species at three levels of aggregation: wetland, lake, and region.

All three attribute variables are related (each pair of attributes is significantly correlated, $p < 0.05$, with correlation coefficients of: $\rho = 0.605$ for MC and THC, 0.351 for MSS and MC, and 0.532 for MSS and THC), just as Curtis and McIntosh's (1951) importance value was based on three related measures of abundance (basal area, density, frequency). However, the three attribute variables have properties that can differentiate dominance behavior. For example, two species might have the same MC, but different THC. One species could usually occur at medium cover while another occurs in concentrations of high cover, called global versus local dominants by Olff and Bakker (1998). The latter behavior would describe an invasive species beginning to overtake an area, while the former would describe a native species with a stable population; therefore, it is useful to distinguish MC from THC. Thus, the simple measurement of cover by species in small plots leads to three attribute variables that, although related, broaden the scope of SDI to include functional (species suppression) and structural (cover and tendency toward high cover) aspects of abundance.

Identifying Dominant Species and Dominance Forms

After computing SDI for each of the potentially dominant species, we selected dominant species as those with SDI values above the mean. Also using the mean of each attribute variable (MC, MSS, THC) as a cut-off, we dichotomized each of the three components of the SDI into "high" and "low" values and differentiated seven forms of dominance (Tables 1 and 2). This allowed us to assign a dominance form to each occurrence of each dominant species. We used the mean value as a cut-off be-

tween "high" and "low" attribute values and between "dominant" and "not dominant" species because the mean is precisely defined and based on the data, but not the total number of potential dominants. Using the mean as a cut-off becomes inappropriate, however, when samples are not distributed along the gradient of environmental conditions. Especially when data sets are small or skewed toward either degraded or pristine conditions, cut-offs may be selected to reflect the system being studied.

The process of determining dominance thus involves; 1) creating a list of potential dominants, 2) computing the SDI, 3) identifying the dominant species, and 4) classifying the dominance forms.

RESULTS

For vegetation with 466 species in the GLEI database, mean SDI found 38 species to be dominant at the wetland scale, 23 to be dominant at the lake scale, and 6 to be dominant at the region scale (Table 3). At the wetland scale, monotype and matrix forms were the most common among species that were dominant in four or more wetlands. Invasive *Typha* (*Typha angustifolia* L. and *Typha* \times *glauca* Godr. combined, narrowleaf and hybrid cattail) and *Phalaris arundinacea* L. (reed canary-grass) showed monotype form more often than matrix form, with monotype:matrix ratios of 14:3 and 5:2, respectively. *Carex stricta* Lam. (upright sedge) and *Calamagrostis canadensis* (Michx.) P. Beauv. (bluejoint grass) had monotype:matrix ratios of 1:1. *Carex lasiocarpa* Ehrh. subsp. *americana* (Fernald) D.Löve and Bernard (wooly-fruit sedge) and *Carex lacustris* Willd. (hairy sedge) showed matrix form more often than monotype form with monotype:matrix ratios of 1:5 and 1:4, respectively. However, *Myrica gale* L. (sweetgale), a shrub, did not show monotype form in any wetland. *Impatiens*

TABLE 2. Seven forms of dominance and the kinds of species that might be associated with them.

Dominance form	Description	“High” variables
Monotype	Frequently influential, few co-occurring species, and high overall abundance. Invasive and transformer species that exist in large monospecific stands fit this form.	MC MSS THC
Ubiquitous	Not frequently influential, but few associated species, and overall high abundance. This form suggests a species that, like the diffuse form (below), is abundant but not often the most abundant. Its low number of co-occurring species suggests the hypotheses that it can achieve high abundance in harsh environments or that a change in condition allows it to become more competitive.	MC MSS
Matrix	Frequently influential, many associated species and high overall abundance. Such species would be common and conspicuous, forming a matrix in which subordinate species flourish. They may be habitat engineers that create niches for a variety of other species, or they might simply occur in areas where subordinate species are good competitors, as in tall grass prairies.	MC THC
Diffuse	Infrequently influential with many associated species, but very common. Such species might grow in many communities and habitats, but only be influential in specific areas.	MC
Compressed	Combines high frequency of influence with few associated species, despite low overall abundance. Due to its overall low abundance, this form might also be patchy, but species with this form would not occur with many other species, suggesting that they grow very densely or in extreme habitats or habitat patches. A species might show this form in the early stages invasion, before it expands	MSS THC
Aberrant	Infrequently influential with low overall abundance, however, few species co-occur. Considered dominant because of its few associated species, this form might suggest opportunistic behavior, a species that is able to quickly take advantage of favorable situations. Annuals might show this form.	MSS
Patchy	Frequently influential, many associated species, and low over-all abundance. Such a species might have a large but open growth form or use a limited resource in a novel way. Sparse shrubs or habitat specialists might show this form. This form could also be the result of an edge effect where a diverse community meets a community with a few species.	THC

capensis Meerb (jewelweed), an annual, never showed matrix form (Fig. 1). Out of 38 dominant species, 19 species showed monotype form, 16 matrix, 13 compressed, 13 patchy, 3 ubiquitous, 2 aberrant, and 1 diffuse.

At the lake scale, only 5 of 23 dominant species were dominant in more than one lake. Of those, only two showed different forms in different lakes. Invasive *Typha* was dominant in four lakes (all but the most northern, Superior), always showing monotype form. *Carex stricta* and *C. lasiocarpa*

were each dominant in two lakes (Huron and Superior, the northernmost lakes), showing matrix form in both lakes. *Calamagrostis canadensis* and *Phalaris arundinacea* were also dominant in two lakes (Michigan and one other), but their dominance forms varied (Fig. 1).

When we examined the entire region as one unit, six dominant species emerged. Invasive *Typha* and *Calamagrostis canadensis* showed monotype form while *Carex lasiocarpa* showed matrix form. *Sagittaria latifolia* Willd. (broadleaf arrowhead) and *Im-*

TABLE 3. Dominant species found at different aggregation levels (number of areas in which a species was dominant). Species names follow the Integrated Taxonomic Information System (www.itis.gov).

Wetland dominants		Lake dominants	Regional dominants
Invasive <i>Typha</i> (22)	<i>Equisetum fluviatile</i> (1)	Invasive <i>Typha</i> (4)	<i>Calamagrostis canadensis</i>
<i>Calamagrostis canadensis</i> (11)	<i>Lythrum salicaria</i> (1)	<i>Calamagrostis canadensis</i> (2)	<i>Carex lasiocarpa</i>
<i>Phalaris arundinacea</i> (8)	<i>Myriophyllum sibiricum</i> (1)	<i>Carex lasiocarpa</i> (2)	<i>Carex stricta</i>
<i>Carex lacustris</i> (6)	<i>Nuphar lutea</i> (1)	<i>Carex stricta</i> (2)	<i>Impatiens capensis</i>
<i>Carex lasiocarpa</i> (6)	<i>Polygonum amphibium</i> (1)	<i>Phalaris arundinacea</i> (2)	<i>Sagittaria latifolia</i>
<i>Carex stricta</i> (4)	<i>Pontederia cordata</i> (1)	<i>Azolla</i> sp. (1)	Invasive <i>Typha</i>
<i>Impatiens capensis</i> (4)	<i>Rhynchospora fusca</i> (1)	<i>Carex lacustris</i> (1)	
<i>Myrica gale</i> (4)	<i>Riccia</i> sp. (1)	<i>Chara vulgaris</i> (1)	
<i>Sparganium eurycarpum</i> (4)	<i>Sagittaria graminea</i> (1)	<i>Equisetum fluviatile</i> (1)	
<i>Nymphaea odorata</i> (3)	<i>Schoenoplectus acutus</i> (1)	<i>Impatiens capensis</i> (1)	
<i>Comarum palustre</i> (2)	<i>Schoenoplectus fluviatilis</i> (1)	<i>Lemna minor</i> (1)	
<i>Lemna minor</i> (2)	<i>Solanum dulcamara</i> (1)	<i>Myrica gale</i> (1)	
<i>Nelumbo lutea</i> (2)	<i>Sparganium erectum</i> (1)	<i>Nelumbo lutea</i> (1)	
<i>Peltandra virginica</i> (2)	<i>Stuckenia pectinatus</i> (1)	<i>Nymphaea odorata</i> (1)	
<i>Sagittaria latifolia</i> (2)	<i>Typha latifolia</i> (1)	<i>Peltandra virginica</i> (1)	
<i>Sphagnum</i> sp. (2)		<i>Phragmites australis</i> (1)	
<i>Thelypteris palustris</i> (2)		<i>Polygonum amphibium</i> (1)	
<i>Urtica dioica</i> (2)		<i>Sagittaria graminea</i> (1)	
<i>Utricularia macrorhiza</i> (2)		<i>Sagittaria latifolia</i> (1)	
<i>Azolla</i> sp. (1)		<i>Sparganium eurycarpum</i> (1)	
<i>Chamaedaphne calyculata</i> (1)		<i>Sphagnum</i> sp. (1)	
<i>Cladium mariscoides</i> (1)		<i>Thelypteris palustris</i> (1)	
<i>Drosera rotundifolia</i> (1)		<i>Urtica dioica</i> (1)	

patiens capensis showed aberrant form, and *Carex stricta* showed patchy form.

DISCUSSION

While ecologists need general terms to discuss vegetation, the increasing availability of consistently-gathered information across large regions allows more quantitative comparison of species behavior than has been possible historically. Involvement of multiple investigators in regional studies also increases the need for consistent use of terms, such as “dominant.” Here, we offer a SDI that allows one to characterize both which species are dominant and how they dominate. The identity and form of dominant species can then be used as an indicator of community condition. Although our research and examples focus on Great Lakes coastal wetlands, SDI is equally applicable in other herbaceous ecosystems and could be adapted for use in forests.

Our determination of dominant species using SDI complements other ways of quantifying dominance and characterizing species. Although SDI returned

the same dominants as the criterion of “species with highest cover” in 95% of wetlands, SDI added the ability to identify a dominant species’ behavior. Furthermore, SDI complements measures of diversity, such as Shannon and Simpson indices (Hurlbert 1971). SDI differs from diversity indices in that it quantitatively classifies an individual species as dominant and characterizes its mode of dominance, while classical diversity indices give the community a single value. Other schemes characterize individual species by placing them into guilds based on their inherent morphological and/or functional characteristics (e.g., Boutin and Keddy 1993). SDI, on the other hand, assigns different behaviors based on how a species grows within a specific ecological context. Therefore, species that were identified as “matrix” by Boutin and Keddy (1993) because they spread clonally could show several different dominance behaviors, including matrix form, depending on how competition and environmental factors affect clonal growth.

SDI identified dominant wetland species at three aggregation scales in the Great Lakes region, differentiating all seven dominance forms (Table 1)

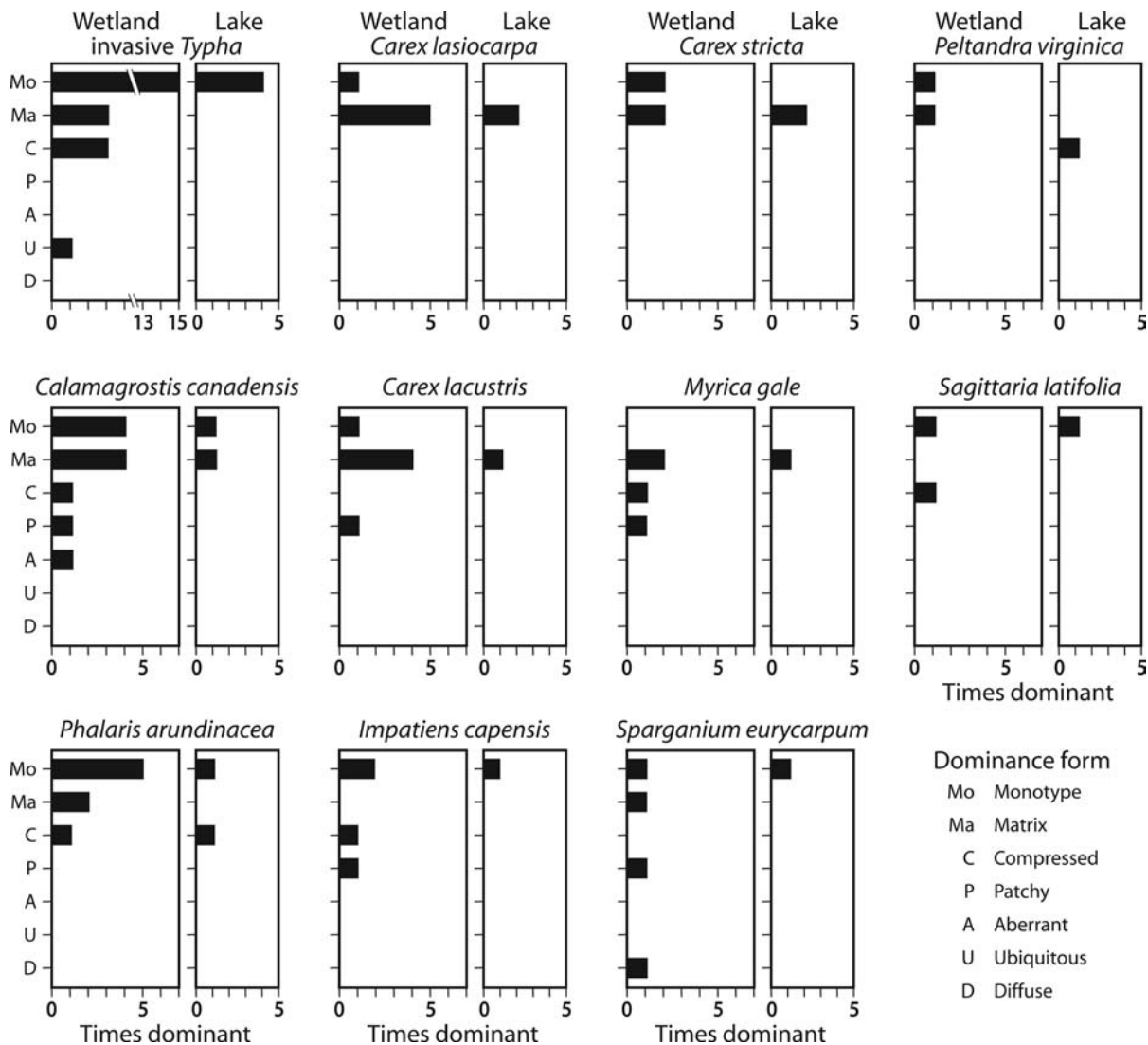


FIG. 1. The number of times a species showed the seven forms of dominance at the wetland and lake scales. Species names follow the Integrated Taxonomic Information System (www.itis.gov).

among Great Lakes coastal wetlands. While forms showing low THC were uncommon in the dataset, these forms and the distinction between high and low THC have utility. For example, THC distinguishes between a species showing monotype form with widespread high cover and few associated species, and one showing ubiquitous form that is widespread with patches of high cover and few associated species. While a species showing ubiquitous form is itself associated with low species richness, the areas where it occurs may still have relatively high overall species richness. For exam-

ple, neighboring Lake Ontario wetlands had 8 species/m² where invasive *Typha* (cattail) showed ubiquitous form compared to 5.4 and 6.5 species/m² where it showed monotype form. Thus the ubiquitous form could serve as a warning of invasion and species richness decline.

As is consistent with our hypothesis, species showed different dominant forms among locations and aggregation scales. Invasive *Typha* was the taxon that was most often dominant in the data. It showed a predominantly monotype form at the wetland scale (20% of wetlands), at the lake scale (80%

of lakes), and at the whole region scale; i.e., its dominance form was relatively stable across scales and locations. In contrast, *Sagittaria latifolia* (broadleaf arrowhead) was dominant at the whole region scale (aberrant form), but was only dominant in one lake and two wetlands, with varying forms (Fig. 1). Despite its infrequent dominance at the smaller aggregation scales, *S. latifolia* was widespread in Lake Erie, and it had high MSS throughout the Great Lakes. Other species, such as *Utricularia macrorhiza* Le Conte (common bladderwort) and *Nymphaea odorata* Aiton (American waterlily), were also dominant in two wetlands but were too infrequent to be dominant at the lake scale.

Several factors might contribute to a species having different dominance forms at different locations within a spatial scale. Given the large geographic range from which these data were collected, climatic differences could account for changes in dominance form. *Calamagrostis canadensis* (blue-joint), for example, is known primarily as a wetland plant of open meadows in southern Wisconsin, but in northern Wisconsin it is much more pervasive, occurring in uplands and forests as well (Leiffers *et al.* 1993). The geomorphic type of wetland is also known to influence vegetation in coastal wetlands (Keough *et al.* 1999).

Environmental conditions and anthropogenic stress could also account for changes in dominance form. Several studies have reported a change in species behavior with changes in environmental condition due to increased anthropogenic stress. Both sedimentation and fertilizer additions give competitive advantages to invasive species in Wisconsin wetlands (Woo and Zedler 2002, Kercher and Zedler 2004). Wisheu *et al.* (1991) indicated a shift in community composition with eutrophication of wetlands. Phosphorus enrichment changed *Eleocharis* sp. (spikerush) density in Belize (Rejmankova 2001) and was linked to the distribution and abundance of *Typha domingensis* (southern cattail) in the Everglades (Vaithianathan and Richardson 1999). Differences in forms of dominance across locations and/or changes in form over time may indicate differences and changes in abiotic attributes of communities such as nutrient availability and sedimentation levels.

SDI shows promise for use as an indicator of community condition and in assessing temporal changes in dominance. For example, in wetlands of Green Bay, Lake Michigan, changing land use can alter environmental conditions, such as nutrient

loading, and annual variations in Lake Michigan water levels change wetland area. Traditional indicators, such as the number of wetland acres, give no information about the quality of the wetlands and could confuse wetland loss with a natural variation in wetland size. The presence or abundance of invasive species has also been suggested as an indicator of wetland quality. However, Denslow and Hughes (2004) note that complex community interactions can allow a blurring of the distinction between native and exotic dominants, as native dominants become management issues and exotic dominants do not always decrease species diversity. Therefore, by using SDI to designate the dominant species and forms, instead of relying on the perceived quality of a species in general, we gain information about the condition of the community and can better differentiate among communities (e.g., Fig. 2).

Our map of Green Bay wetlands (Fig. 2b) illustrates how SDI can be used by managers to show at a glance the variety of species that dominate and the variety of dominance forms they display. A colorful map differs dramatically from one having only black circles (all wetlands dominated by monotypes; not shown). Focusing on invasive *Typha* (cattail), a species of management concern in the region, one could use this baseline map to track its increasing dominance and shifts toward monotypes.

At Long Tail Point Marsh invasive *Typha* (iT) shows matrix form, but it has already become a monotype in Atkinson Marsh. In a survey of Wisconsin's coastal wetlands, Epstein *et al.* (2002) described Atkinson Marsh as degraded and having a simplified vegetative composition; they also noted that the marsh receives copious nutrients and sediments from the Fox River. In contrast, they described Long Tail Point Marsh as containing a good quality emergent marsh dominated by cattails (*Typha*) and bulrushes. From the descriptions of Epstein *et al.* (ibid), it is clear that there are important differences between the marshes, even though both are dominated by *Typha*. These differences are revealed by the dominance form designation provided by the SDI framework.

At Point au Sable, SDI designated invasive *Typha* as showing the compressed form of dominance. This situation could be a red flag for managers to investigate the condition of this wetland and adjacent land uses. When the data were collected from Point au Sable, invasive *Typha* was rare within the large and recently exposed lagoon; thus, it had low MC and showed compressed rather than monotype form. In 2001, we were concerned that *Typha*

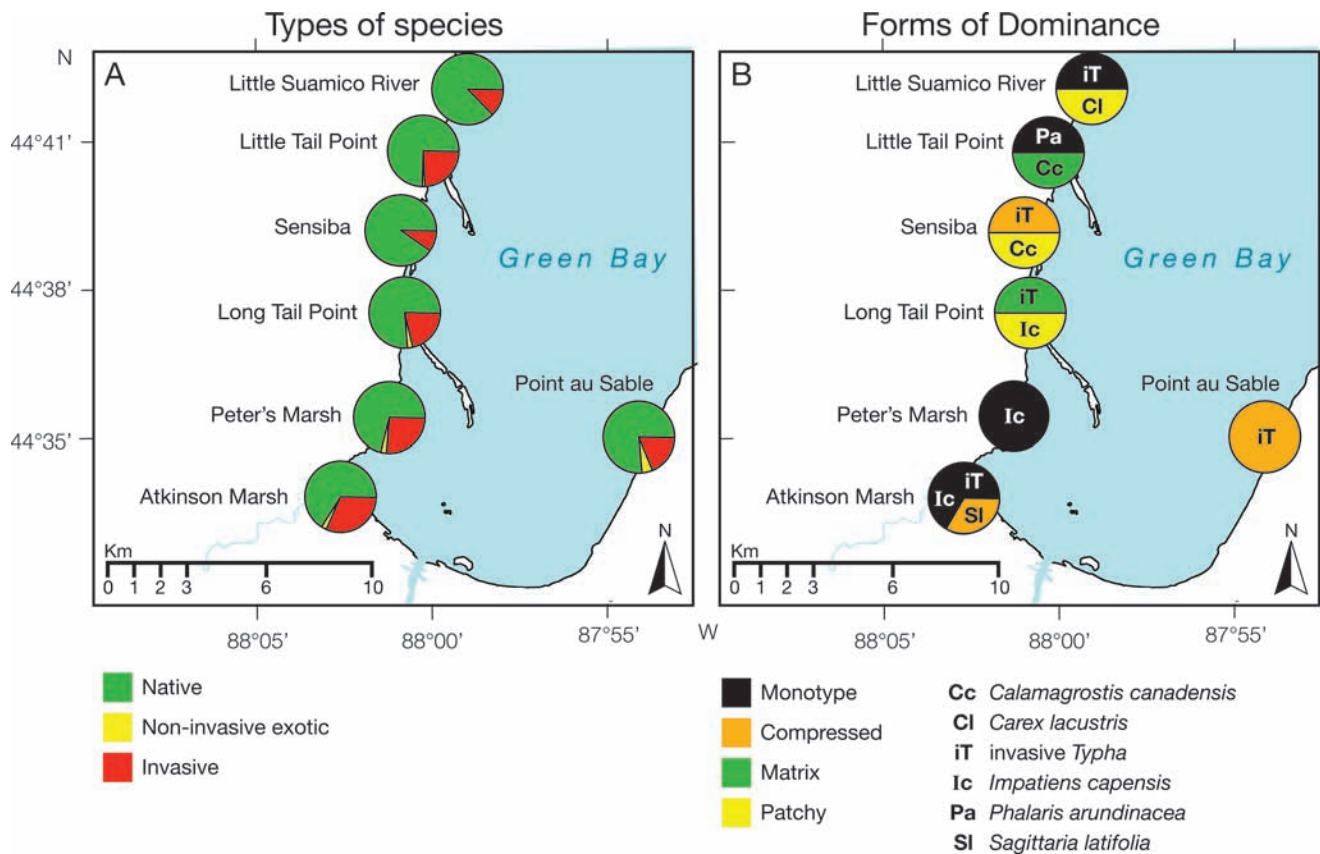


FIG. 2. An example of the utility of SDI showing the characterization of wetlands along Wisconsin's Green Bay coast: (a) percentage of quadrats occupied by native, non-invasive alien, and invasive species, and (b) proportion of dominant species showing different dominance forms as determined using SDI; two letter codes indicate the identity of the dominant species.

would invade the lagoon and develop a monotype. In recent years, however, this wetland was overtaken by another invasive, *Phragmites australis* (Cav.) Trin. ex Steud. (common reed; CAJ pers. obs.). If managers were using SDI as a red flag in 2001, they might have caught the new invasion before it became so extensive.

We anticipate that SDI will have utility as an objective indicator of condition over time. SDI could be used to track the effectiveness of measures to control invasive species, the progress of restoration, and degradation over time. For example, *Phragmites australis* has expanded rapidly in many Green Bay wetlands since our data were collected (CBF pers. obs.). Resampling and applying SDI to the results would give managers a quantitative measure of the changes in both dominant species and dominance form resulting from the *Phragmites* invasion,

and the updated map would show more black circles.

The seven forms of dominance comprise a useful framework with more than theoretical value. The forms are easily defined and have practical application; they represent ecological traits that integrate species identity, environmental conditions, and geographical location. Our analytical approach is adaptable for use with many different abundance measures and vegetation types, it provides clarity and objectivity to an intuitive concept, and it helps suggest mechanisms responsible for differences in dominance within and among species.

ACKNOWLEDGMENTS

This research was supported by a grant from the U.S. Environmental Protection Agency's Science to Achieve Results Estuarine and Great Lakes program through funding to the Great Lakes Environ-

mental Indicators project, cooperative agreement EPA/R-82867501 (Gerald Niemi, principal investigator). Although the research described in this article has been funded in part by the United States Environmental Protection Agency, it has not been subjected to the agency's required peer and policy review and therefore does not necessarily reflect the views of the agency and no official endorsement should be inferred. Support also came from the Wisconsin Coastal Management Program, administered by the National Oceanic and Atmospheric Administration contract 84003-004.40 and, for CAJ, from National Science Foundation/EPSCoR Grant #EPS-0091948.

Data for Lake Michigan wetlands were collected by C. Frieswyk with Aaron Boers, Spencer Cronk, and Laura Ladwig; Lakes Superior and Huron by Michael Aho, Michael Bourdaghs, Terry Brown, Charlene Johnson, and Mirela Tulbure; and Lakes Ontario and Erie by Kathy Bailey and Lynn Vaccaro. In addition, we thank Barbara Bedford, Terry Brown, Michael Bourdaghs, and Lynn Vaccaro for discussion and development of sampling methods.

REFERENCES

- Abella, S.R., and Covington, W.W. 2004. Monitoring an Arizona ponderosa pine restoration: Sampling efficiency and multivariate analysis of understory vegetation. *Restor. Ecol.* 12:359–367.
- Allison, S.D., and Vitousek, P.M. 2004. Rapid nutrient cycling in leaf litter from invasive plants in Hawaii. *Oecologia* 141:612–619.
- Bardgett, R.D., Maludsley, J.L., Edwards, S., Hobbs, P.J., Rodwell, J.S., and Davies, W.J. 1999. Plant species and nitrogen effects on soil biological properties of temperate upland grasslands. *Func. Ecol.* 13:650–660.
- Boutin, C., and Keddy, P.A. 1993. A functional classification of wetland plants. *J. Veg. Sci.* 4: 591–600.
- Braun-Blanquet, J. 1932. *Plant sociology: the study of plant communities*. New York, New York: McGraw-Hill Book Company, Inc.
- Carpenter, J.R. 1956. *An ecological glossary*. New York, New York: Hafner Publishing Company.
- Clark, J.S., Grimm, E.C., Lynch, J., and Mueller, P.G. 2001. Effects of Holocene climate change on the C-4 grassland/woodland boundary in the northern plains, USA. *Ecology* 82:620–636.
- Clements, F.E. 1916. *Plant succession*. Washington, District of Columbia: Carnegie Institution of Washington.
- Curtis, J.T., and McIntosh, R.P. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32:476–496.
- Dangles, O., and Malmquist, B. 2004. Species richness-decomposition relationships depend on species dominance. *Ecol. Lett.* 7:395–402.
- Danz, N.P., Regal, R.R., Niemi, G.J., Brady, V., Hollenhorst, T., Johnson, L.B., Host, G.E., Hanowski, J.M., Johnston, C.A., Brown, T., Kingston, J., and Kelly, J.R. 2005. Environmentally stratified sampling design for the development of Great Lakes environmental indicators. *Environ. Monit. Assess.* 102:41–65.
- Denslow, J.S., and Hughes, R.F. 2004. Exotic plants as ecosystem dominants. *Weed Technol.* 18:1283–1287.
- Epstein, E., Spencer, E., and Feldkirchner, D. 2002. *A data compilation and assessment of the coastal wetlands of Wisconsin's Great Lakes*. Dept. of Natural Resources, Wisconsin's Natural Heritage Inventory Program, Madison, Wisconsin. PUBL ER-803 2002.
- Fastie, C.L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology* 76:1899–1916.
- Galatowitsch, S.M., Anderson, N., and Ascher, P. 1999. Invasiveness in wetland plants in temperate North America. *Wetlands* 19:733–755.
- Godefroid, S., and Koedam, N. 2003. Identifying indicator plant species of habitat quality and invasibility as a guide for peri-urban forest management. *Biodivers. Conserv.* 12:1699–1713.
- Greig-Smith, P. 1986. Chaos or order—organization. In *Community ecology: pattern and process*, J. Kikkawa and D.J. Anderson, eds., pp. 19–29. Melbourne, Australia: Blackwell Scientific Publications.
- Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86:902–910.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38:210–221.
- Hector, A., Bazeley-White, E., Loreau, M., Otway, S., and Schmid, B. 2002. Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. *Ecol. Lett.* 5:502–511.
- Hodgson, J.G., Thompson, K., Wilson, P.J., and Bogaard, A. 1998. Does biodiversity determine ecosystem function? The Ecotron experiment reconsidered. *Func. Ecol.* 12:843–848.
- Howe, H.F., and Brown, J.S. 1999. Effects of birds and rodents on synthetic tallgrass communities. *Ecology* 80:1776–1781.
- Hurlbert, S.H. 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52:577–586.
- Keough, J.R., Thompson, T.A., Guntenspergen, G.R., and Wilcox, D.A. 1999. Hydrogeomorphic factors and ecosystem responses in coastal wetlands of the Great Lakes. *Wetlands* 19:821–834.
- Kercher, S.M., and Zedler, J.B. 2004. Multiple disturbances accelerate invasion of reed canary grass

- (*Phalaris arundinacea* L.) in a mesocosm study. *Oecologia* 138:455–464.
- , Frieswyk, C.B., and Zedler, J.B. 2003. Effects of sampling teams and estimation methods on the assessment of plant cover. *J. Veg. Sci.* 14:899–906.
- Lavoie, C., Jean, M., Delisle, R., and Létourneau, G. 2003. Exotic plant species of the St. Lawrence River wetlands: a spatial and historical analysis. *J. Biogeogr.* 30:537–549.
- Leiffers, V.J., Macdonald, S.E., and Hogg, E.H. 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. *Can. J. Forestry Res.* 23:2070–2077.
- Ludwig, J.A., Tongway, D.J., Bastin, G.N., and James, C.D. 2004. Monitoring ecological indicators of range-land functional integrity and their relation to biodiversity at local and regional scales. *Austral Ecol.* 29:108–120.
- Malmer, N., Albinsson, C., Svensson, B.M., and Wallin, B. 2003. Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. *Oikos* 100:469–482.
- Olf, H., and Bakker, J.P. 1998. Do intrinsically dominant and subordinate species exist? A test for field data. *Appl. Veg. Sci.* 1:15–20.
- Potvin, C., and Vasseur, L. 1997. Long-term CO₂ enrichment of a pasture community: species richness, dominance, and succession. *Ecology* 78:666–677.
- Rabinowitz, D. 1981. Seven forms of rarity. In *The biological aspects of rare plant conservation*, H. Synge, ed., pp. 205–217. Chichester, United Kingdom: John Wiley & Sons Ltd.
- Rejmankova, E. 2001. Effect of experimental phosphorus enrichment on oligotrophic tropical marshes in Belize, Central America. *Plant Soil* 236:33–53.
- Richards, P.W. 1996. *The tropical rainforest: an ecological study*. Cambridge, United Kingdom: Cambridge University Press.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., and West, C.J. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib.* 6:93–107.
- Robinson, G.R., Quinn, J.F., and Stanton, M.L. 1995. Invasibility of experimental habitat islands in California winter annual grassland. *Ecology* 76:786–794.
- Simberloff, D., and Von Holle, B. 1999. Positive interactions of non-indigenous species: invasional meltdown? *Biol. Invasions* 1:21–32.
- Smith, M.D., and Knapp, A.K. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.* 6:509–517.
- Taylor, A.H. 2000. Fire regimes and forest changes in mid and upper montane forest of the southern Cascades, Lassen Volcanic National Park, California, USA. *J. Biogeogr.* 27:87–104.
- Theodose, T.A., and Bowman, W.D. 1997. Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. *Ecology* 78:1861–1872.
- Vaithianathan, P., and Richardson C.J. 1999. Macrophyte species changes in the Everglades: examination along a eutrophication gradient. *J. Environ. Qual.* 28:1347–1358.
- van der Valk, A.G. 1981. Succession in wetlands: a Gleasonian approach. *Ecology* 62:688–696.
- Walker, B., Kinzig, A., and J. Langridge, J. 1999. Plant attribute diversity, resilience and ecosystem function: the significance of dominant and minor species. *Ecosystems* 2:95–113.
- Whittaker, R.H. 1965. *Communities and ecosystems*. New York, New York: MacMillan Publishing Co., Inc.
- Wisheu, I.C., and Keddy, P.A. 1992. Competition and centrifugal organization of plant communities: theory and tests. *J. Veg. Sci.* 3:147–156.
- , Keddy, P.A., Moore, D.R.J., McCanny, S.J., and Gaudet, C.L. 1991. Effects of eutrophication on wetland vegetation. In *Wetlands of the Great Lakes (protection and restoration policies: status of the science)*, pp. 112–121. New York, New York: Managers Inc.
- Woo, I., and Zedler, J.B. 2002. Can nutrients alone shift a sedge meadow towards dominance by the invasive *Typha × glauca*? *Wetlands* 22:509–521.

Submitted: 31 July 2006

Accepted: 8 May 2007

Editorial handling: Gerald J. Niemi